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ACHENE MORPHOLOGY, PRODUCTION AND GERMINATION, AND POTENTIAL FOR WATER DISPERSAL IN *BOLTONIA DECURRENS* (DECURRENT FALSE ASTER), A THREATENED FLOODPLAIN SPECIES

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ABSTRACT. The decurrent false aster, *Boltonia decurrens* (Asteraceae), is a Federally listed, threatened floodplain species endemic to a 400 km reach of the lower Illinois River and adjacent areas of the Mississippi River. The present study was conducted in response to the Recovery Plan for *B. decurrens,* which called for life history studies to provide information essential to planning management programs for the species. A series of laboratory studies was conducted to determine achene morphology, achene production and germination under a variety of conditions, and the potential for dispersal by water. *Boltonia decurrens* produces ca. 50,000 achenes per individual, and based on achene viability observed in this study, an average plant is capable of producing ca. 40,000 seedlings under optimal conditions for germination. There was no difference between germination of achenes produced by ray and disk florets; however, achene size had a significant effect on germination and viability, with larger achenes having higher levels of both. Achenes are morphologically adapted for flotation, and germination was not significantly reduced in achenes floated for four weeks. Achenes which were not exposed to light did not germinate, whether they were covered with aluminum foil or with sediment. Results suggest that factors other than fecundity are responsible for the threatened status of *B. decurrens.* Heavy siltation of river water caused by agricultural runoff, and flood control measures limiting dispersal may have contributed to the decline of the species.

Key Words: life history, threatened species, management, floodplain

The decurrent false aster, *Boltonia decurrens* (Torr. and Gray) Wood (Asteraceae), a Federally listed, threatened floodplain species (U.S. Fish and Wildlife Service 1988), occurs along a 400 km section of the lower Illinois River and nearby parts of the Mississippi River (Schwegman and Nyboer 1985; U.S. Fish and Wildlife Service 1990). *Boltonia decurrens* is an early successional species that requires either natural or human disturbance to create and maintain suitable habitat. Its natural habitat was wet prairies, shallow marshes, and shores of open rivers, creeks, and lakes (Schwegman and Nyboer 1985). In the past, the annual flood/drought cycle of the Illinois River provided the natural disturbance required by this species. Annual spring flooding created open, high-light habitat and reduced competition by killing other, less flood-tolerant, early successional species. Field observations indicate that in "weedy" areas without disturbance, the species is eliminated by competition within three to five years (U.S. Fish and Wildlife Service 1990). *Boltonia decurrens* has high light requirements for growth and achene germination (Smith et al. 1993; Smith et al. 1995), and shading from other vegetation is thought to contribute to its decline in undisturbed areas.

Boltonia decurrens also exhibits morphological adaptations for life on the floodplain. Stoecker et al. (1995) found *B. decurrens* to be extremely tolerant when maintained under conditions of root-zone saturation. All plants in the flood treatment survived to study completion at 56 days. The formation of aerenchyma, a common plant adaptation to flooding which allows diffusion of oxygen from aerial shoots to maintain root metabolism (Armstrong 1971; Crawford 1978; Laan et al. 1990), was extensive, increasing in adventitious roots from 26% of root cross section area in non-flooded plants to 49% in flooded plants (Stoecker et al. 1995).

Boltonia decurrens reproduces vegetatively and sexually. Vegetative production of one or more basal rosettes occurs during the fall. Rosettes bolt the following spring; plants flower and set achenes from late August to early October. Field monitoring by Schwegman and Nyboer (1985) suggested prolific achene production. Fall seedlings overwinter, and bolt and flower the following spring and summer. Spring seedlings, however, may either bolt and flower the same year or overwinter as small rosettes which bolt and flower the following year (Smith 1991). In areas where seedling production is low or nonexistent, *B. decurrens* populations can be maintained by basal rosette production. In fact, few seedlings are found in established populations (Moss 1997; Smith 1991). Seedling establishment is expected to be low due to the small achene size, the high light and temperature requirements for germination, and specific soil texture and microtopography requirements for germination and seedling growth (Baskin and Baskin 1988; Smith et al. 1995). The present study was conducted to determine the potential fecundity of *B. decurrens* and to examine the adaptive life history characteristics which enhance achene dispersal and survival on the floodplain.

MATERIALS AND METHODS

All achenes and plants used in this study were collected from a population near the Melvin Price Locks and Dam, St. Charles County, Missouri (lat. 38°52′06″N, long. 90°12′22″W; elev. 140 m). The height of 85 plants, every third plant along a transect, was measured and plants numbered on 12 Oct 1989. Eighty of the marked plants were collected on 2 Nov 1989, and transported to SIUE where total biomass was measured and inflorescences counted. Achenes for all germination experiments were collected on 3 Nov 1989.

Potential fecundity. Inflorescences on each plant were counted, and achenes per inflorescence were counted for a random subsample of 100 inflorescences. Potential fecundity was calculated as the average number of achenes per inflorescence × number of inflorescences for each plant. Shoots and roots were separated, dried at 80°C for four days, and then weighed. Correlations were calculated by the method of least squares (Sokal and Rohlf 1981) using Sigma Stat 2.0 (Jandel Scientific Software, San Rafael, CA), and the coefficient of correlation and statistical significance determined for the following combination of paired, random variables: plant height and potential fecundity (achene number per plant); total dry weight and potential fecundity; above ground dry weight and potential fecundity; and root dry weight and potential fecundity.

Germination of ray and disk achenes. A dissecting microscope (at 25×) was used to examine 100 inflorescences to determine the ratio of ray flowers to disk flowers and to compare achene mass, size, and morphology. Mass of each achene type was determined by weighing 200 of each on a Sartorius (Model L 420D) balance and calculating the mean weight per achene. Size (length, width, and height) of ten of each type of achene was measured using a dissecting microscope and a mm ruler. Three hundred achenes (30 achenes × 10 dishes) of each type were placed on filter paper in plastic petri dishes, soaked with deionized water, sealed in ZipLoc bags and placed at a randomly assigned position in a Conviron E-15 environmental chamber at 25°C, 75% relative humidity, 900 μMol m^{-2} s^{-1} Photon Flux Density and 12/12 h day/night cycle. For four weeks, at weekly intervals, achene germination was determined by emergence of the radicle. Statistical difference in germination between the two types was analyzed using Fisher's Exact Test (Sokal and Rohlf 1981). Statistical differences were inferred when $P < 0.05$. In addition, mass of each achene type was determined by weighing 200 of each and calculating the average weight per achene.

Size-related achene germination. A random sample of achenes was selected and separated into two size classes using a 0.5 mm screen filter (U.S.A. standard testing sieve, Fisher Scientific Co.). Six hundred large and 600 small achenes were separated into 12 lots of 100 each and placed on filter paper in petri dishes. To test for germination, six lots of 100 were incubated in deionized water only and the remaining six lots were treated with 0.5% tetrazolium chloride to determine viable, but dormant, achenes (Zhang and Maun 1989). All achenes were maintained in the environmental chamber, at conditions previously described, for three weeks. At the beginning of week 4, temperature in all treatments was raised to 35°C. All results were tested for significant differences (germination and viability) between the two size classes using Fisher's Exact Test (Sokal and Rohlf 1981).

Germination in darkness. Four replicate lots of 100 achenes each were randomly selected, placed on filter paper in plastic petri dishes, and soaked with deionized water. The petri dishes were wrapped in two layers of aluminum foil and placed in the environmental growth chamber for four weeks, with conditions as described above.

Germination of sediment covered achenes. Soil from the study population site was cleaned of large roots and rocks and sterilized. A 1.5 cm layer of sterile Promix potting soil was placed in 10 cm^2 pots and topped with 3.5 cm of sterilized site soil. This mixture was saturated with deionized water, 50 achenes placed in each pot, and covered with a layer of "silt" (site soil that had been mixed with deionized water in a Waring blender until it was the consistency of river silt). Four pots were used per treatment, with achenes placed at each of the following depths of silt: 0 cm (exposed), 0.5 cm, 1.0 cm, 1.5 cm, 2.0 cm, and 2.5 cm. Pots were placed in trays, watered, and covered with plastic wrap to retard the formation of a hard surface film. All treatments were maintained in the environmental growth chamber for four weeks, with conditions as previously noted. Germination was determined by emergence of hypocotyl and primary leaves.

Flotation and germination of achenes. One hundred disk achenes each were placed in three 250 ml Erlenmeyer flasks filled with 150 ml deionized water. Achenes were gently washed down from the sides of the flask once weekly with a pipette. At the end of the third week, one flask was placed on a shaker table for one week to simulate possible wave action. The number of floating achenes was counted weekly, and at the end of week 4 the achenes were placed on filter paper in plastic petri dishes, soaked with deionized water, sealed in ZipLoc bags and placed in an environmental growth chamber, with conditions as previously noted. Statistical difference in germination between the two treatments was analyzed using Fisher's Exact Test (Sokal and Rohlf 1981). Statistical differences were inferred when $P < 0.05$.

RESULTS

Potential fecundity. Plant height, biomass, and achene production were highly variable in this naturally occurring population (Table 1). Data analysis indicated positive correlations between inflorescence production and shoot dry weight ($r = 0.97$), root dry weight ($r = 0.94$), total dry weight ($r = 0.97$), and shoot height ($r = 0.88$; Table 2). Potential fecundity of the average whole plant (inflorescences/whole plant × achenes/inflorescence) was 51,121, or 26,923 for the mean individual shoot (inflorescences/individual shoot × achenes/inflorescence).

Germination of ray and disk achenes. Examination of inflorescences revealed that ray and disk flowers are morphologically distinct: disk flowers are perfect (bisexual), fertile, and yellow; ray flowers are pistillate, fertile, and vary from white to pink or pale purple. Both flower types appear to set seed routinely, producing achenes that differ significantly in size (Table 3). In addition, disk achenes have two prominent, stiff bristles emerging

Table 1. Plant height, dry weight (g DWT), and achene production for individual shoots and whole plants of *Boltonia decurrens.* * Root systems produced variable numbers of shoots. Each individual shoot was measured for height, dry weight, and achene production. ** Mean height, dry weight, and achene production were calculated for the shoots associated with each root system.

Character	Mean	SD	n
*Shoot height/individual (cm)	107.3	39.1	142
**Total shoot height/whole plant (cm)	204.1	210.2	80
Above-ground biomass/shoot (g DWT)	11.3	14.6	142
Above-ground biomass/whole plant (g DWT)	24.5	67.3	80
Root biomass (g DWT)	4.6	5.2	80
Total biomass/whole plant (g DWT)	29.1	75.3	80
Inflorescences/individual shoot	109.4	121.9	
Inflorescences/whole plant	207.8	367.9	
Achenes/inflorescence	247.4	49.3	100

from the base of the achene (remnant of the pappus). During flotation experiments, these bristles were observed to have small air bubbles clinging to them. The disk to ray flower ratio (4.3:1) was consistent in both large and small inflorescences. At this ratio, the number of each type of achene produced by an "average" plant (Table 1) would be ca. 41,475 disk achenes and 9645 ray achenes. Percent germination did not differ significantly between achene types.

Size-related germination and viability. Achene size had a significant effect on germination and viability (Table 4), with larger achenes having significantly greater ($P < 0.05$) percentages of both germination and viability. Viability of both size classes was significantly greater ($P < 0.001$) than germination. The effect

Table 2. Correlation coefficient (r) for Shoot Dry Weight (SDWT), Root Dry Weight (RDWT), Total Dry Weight (TDWT), and Shoot Height (HT) versus Number of Inflorescences (#INF) for individuals of *Boltonia decurrens* in the study. n = 80 for all parameters.

Characteristic	r	Significance (P-value)
SDWT × #INF	0.97	<0.001
RDWT × #INF	0.94	<0.001
TDWT × #INF	0.97	<0.001
HT × #INF	0.88	<0.001

Table 3. Number of disk and ray achenes per inflorescence; mass of both types; size (L = length, W = width, H = apical hair length); and percent germination. Sample sizes reflect numbers per each achene type. Values in rows with different letters (a,b) are significantly different ($P < 0.05$). Statistical differences for achene size were determined by Student's t test and for germination by Fisher's Exact Test. * Mass of each achene type was determined by weighing 203 achenes of each type and calculating the average. — Prominent hairs not present.

Characteristic	Disk Achenes	Ray Achenes	Sample Size
#/Inflorescence (SD)	223.4(44.5)[a]	52.0(11.1)[a]	100
*Mass (g $\times 10^{-5}$)	6.5	4.9	203
L (mm) (SD)	1.8 (0.1)[a]	1.3 (0.1)[b]	10
W (mm) (SD)	1.3 (0.1)[b]	0.9 (0.1)[b]	10
H (mm) (SD)	0.9 (0.2)	—	10
% Germination	62.1(12.2)[a]	68.0(13.5)[a]	300

of temperature on germination, however, was not statistically significant.

Germination in darkness. Of the 400 achenes in the dark treatment, one germinated (0.25%).

Germination of sediment covered achenes. Forty percent of the achenes placed on the sediment surface germinated during the 4-week observation period. With a single exception (1 achene at 1.0 cm sediment depth), no achenes germinated when covered with 0.5 to 2.5 cm of sediment (Table 5).

Table 4. Germination and viability in large and small achenes of *Boltonia decurrens* after 3 and 4 weeks. Figures in rows with different letters (a,b) are significantly different ($P < 0.001$) as determined by Fisher's Exact Test. *All values for comparisons among large vs. small achenes were significantly different ($P < 0.05$) as determined by Fisher's Exact Test. n = 300 for each experiment.

Achene Size	% Germination	% Viability
*Large (>0.5 mm)		
Week 3 (25°C)	37.6[a]	77.6[b]
Week 4 (35°C)	42.0[a]	83.0[b]
*Small (<0.5 mm)		
Week 3 (25°C)	29.3[a]	69.3[b]
Week 4 (35°C)	32.3[a]	74.0[b]

Table 5. Germination of achenes of *Boltonia decurrens* located on the soil surface or buried under one of five depths (0.5 cm, 1.0 cm, 1.5 cm, 2.0 cm, and 2.5 cm) of silt for 4 weeks. n = 200 for each treatment.

Siltation Depth (cm)	% Germination
0	40
0.5	0
1.0	0.5
1.5	0
2.0	0
2.5	0

Flotation and germination of achenes. The percent germination of achenes which had been floated for 4 weeks was within the range observed in other portions of the study (Tables 4, 5, and 6). Three achenes (1.5%) germinated while still in the water. There was a significant reduction ($P < 0.001$) in the number of achenes floating after 4 weeks that had been shaken (to simulate wave action) when compared to those floating on still water. There was no significant difference ($P < 0.051$) in percent germination of achenes in still water when compared to achenes that were shaken to simulate wave action.

DISCUSSION

Boltonia decurrens is a prolific achene-producer with a potential fecundity of an average of ca. 50,000 achenes per mature individual. Comparisons of inflorescence production with shoot dry weight, root dry weight, total dry weight, and shoot height indicate that larger, more robust plants produce more achenes. This may be an important consideration in natural populations, because there are two distinctive size groups of individuals: flowering plants produced from vegetative rosettes, which are large

Table 6. Flotation and germination for achenes of *Boltonia decurrens* after 4 weeks in deionized water in laboratory flasks. Figures in columns with different letters (a,b) are significantly different ($P < 0.05$) as determined by Fisher's Exact Test. *Includes 3 achenes which germinated while floating.

Treatment	% Floating	% Germination	n
Stationary Flask	71[a]	*47	200
Shaken Flask	20[b]	39	100

(1–2 m), and flowering individuals produced from spring-germinated seedlings, which are often less than 0.75 m in height (M.S., pers. obs.). Populations established in the first year following a severe flood are composed solely of seedling-derived flowering plants; however, populations in the second year of succession, or in areas where a disturbance wasn't severe enough to eliminate all previous plants, are composed of a mixture of plant types. The population in the present study was composed of a mixture of both flowering types. To determine reproductive potential of any single population in any given year, the composition of the population must be assessed in terms of the two reproductive types of flowering individuals.

It is clear from the results of this study that larger achenes have higher germinability and viability than smaller achenes (Table 4). The test for embryo viability indicated that many achenes remained viable, but dormant, under the light and temperature regimes used in this study. If dormancy were broken by an optimal temperature regime or cold stratification (Baskin and Baskin 1988), percent germination could potentially have risen from ca. 39% to ca. 79%.

Achenes of *Boltonia decurrens* often germinate in the fall, before stratification occurs; therefore, the potential exists for significant seedling establishment during fall and early winter. Estimating an initial germination of 39% of all freshly produced achenes, one could project a mean production of ca. 20,000 seedlings per average plant in the fall. Recent studies in our laboratory (Moss 1997), however, indicate that seedling mortality in the field was extremely high (99.99%) for fall and early winter seedlings at Horseshoe Lake, Madison County, Illinois, during 1995 and 1996.

Under warmer spring and summer temperatures, the remaining 40% of the total achene crop could germinate, providing an additional 20,000 seedlings per plant. In 1995, a year in which flood waters inundated the Horseshoe Lake area until late June, Moss (1997) reported 0.1% survival for spring and summer seedlings, resulting in the production of ca. 20 seedlings per average individual which had flowered the previous fall. Seedling production and survival undoubtedly depend heavily on site conditions, and seedling establishment would vary between years and among sites. This information may help explain the extremely large fluctuations known to occur in population sizes between years (U.S. Fish and Wildlife Service 1990).

An examination of sediment characteristics of Illinois River Valley soil and the sediment load and transparency of flood waters suggests some potential insights into the threatened status of *Boltonia decurrens.* Lee and Stall (1976a) made theoretical calculations of the annual sediment loss in the Illinois River Basin of 25 million metric tons (mmt) or 3.34 mt/ha. About 11 mmt of sediment are annually transported out of the Illinois Valley to the Mississippi River at Grafton, leaving 14 mmt deposited in the water areas and certain unleveed areas of the floodplain. Most transport of sediment occurs during high discharge (Lee and Bhowmik 1979). By removing about half of the floodplain from inundation by the river, drainage and levee districts have increased flood heights and the deposition of sediments on the remaining lakes and unleveed floodplain of the Illinois Valley (Bellrose et al. 1979, 1983). Lee and Stall (1976a) found that sediments deposited in the Illinois River Valley were made up almost equally of silt and clay particles with insignificant amounts of sand.

The present study of *Boltonia decurrens* demonstrated that achenes will not germinate in the dark. Of the 400 achenes in foil-covered dishes, only one germinated. Although one might infer that 0.25% of the achenes of *B. decurrens* will germinate in the dark, these results were more likely caused by a pinpoint of light penetrating the aluminum foil covering the petri dishes (by the end of the study, several very small holes had developed along creases in the foil). In addition, achenes which were covered with as little as 0.5 cm of sediment did not germinate; therefore, if achenes are deposited by flood waters and subsequently covered by a shallow layer of sediment, it is unlikely they will germinate. Natural or human disturbance of the soil, exposing the achenes to light, would be required for germination. This inference is consistent with the recent historical restriction of populations of *B. decurrens* to human-disturbed, agricultural settings (Schwegman and Nyboer 1985).

Sediment type may also be an important factor in achene germination and long-term survival of populations. *Boltonia decurrens* populations have been observed growing on a variety of soil types (Schwegman and Nyboer 1985; Smith 1991); however, laboratory studies (Smith et al. 1995) comparing achene germination and growth on two soil types, silty clay (6.7% sand, 53.3% silt, and 40% clay) and loamy sand (80% sand, 16.7% silt, and 3.3% clay) indicate that germination and seedling growth were significantly greater on sand than on clay. These laboratory results suggest that the silt and clay sediment being deposited by flood events (Lee and Stall 1976b) is not ideal for germination and growth. Soil type may thus be important in determining the distribution pattern of this species.

Water clarity may affect survival and growth of both seedlings and basal rosettes. Achenes of *Boltonia decurrens* are capable of germination in both fall and spring (Moss 1997; Smith 1991). If germination is followed by a flood which reduces water clarity for an extended time period, the new seedlings, even if not washed away (Moss 1997), will likely die due to lack of adequate light for growth (Smith et al. 1993, 1995). Basal rosettes have been observed (M.S. and T.M.K., pers. obs.) to bolt and grow under water when the water was clear, with plants emerging above the water surface and subsequently flowering. This has not been observed in turbid flood waters of the Illinois River. The high light requirements of *B. decurrens* (Smith et al. 1993) would not be met under turbid flood waters.

Achenes of *Boltonia decurrens* are morphologically structured for flotation, and therefore, presumably are adapted for dispersal on river currents. The hairs which emerge from the base of the disk achene trap and hold an air bubble, and the light, thin, broad achene is easily borne on water surfaces. In this study, there was no significant difference in percent germination of achenes which had been floated for 4 weeks and those in other portions of the study, and 20% of achenes floated under condition of simulated wave action were still floating after four weeks. These data indicate that achenes of *B. decurrens* have the potential for long distance dispersal on water.

In the field, there is indirect evidence of dispersal by water. *Boltonia decurrens* has been observed growing in a series of windrows, parallel to the shoreline at Meredosia Lake and Smith Lake, Cass and Morgan Counties, respectively, Illinois (T.M.K. and M.S., pers. obs.). Achenes were deposited on the shoreline by wind-generated waves, and the observed distribution pattern resulted from separate dispersal events as the lake water level receded after flooding. Such observations demonstrate that water dispersal occurs under natural conditions.

Although achenes are apparently adapted for water dispersal, much of the Illinois River Valley is isolated from the river by drainage and levee districts. The levee systems provide an effective barrier to achene dispersal landward of the levee system, except during major floods when the levees are overtopped. In essence, suitable habitat for the species is unavailable because of the levee systems.

The effect of the failure of the species to disperse freely to recently flooded areas is compounded by its apparent inability to compete with other vegetation as succession progresses (Schwegman and Nyboer 1985; Smith et al. 1993). Populations isolated landward of the levee do not experience the annual flood/drought cycle that is necessary to eliminate species which compete for light and suitable germination sites. Without periodic reduction of competing vegetation, *Boltonia decurrens* does not persist for more than five years at any one site.

Studies of basic life history characteristics of threatened and endangered species are necessary to understand the circumstances contributing to their status. While it is impossible to re-create the floodplain system that supported such species, it is possible that knowledge of factors critical to their survival will enable agencies to prevent their extinction through the formulation and implementation of well-designed management plans. The feasibility of substituting alternative site disturbance such as disking, mowing, burning, or controlled flooding should be investigated to determine if it is possible to successfully manage *Boltonia decurrens*, and therefore, to reverse the current population decline.

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